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ALARM VOCALIZATIONS OF COLUMBIAN GROUND SQUIRRELS (Spermophilus
columbianus)

by



David F. Lickley

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
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Abstract

Vocalizations given by Columbian ground squirrels (*Spermophilus columbianus*) in response to the release of trained raptors and dogs were recorded during the summers of 1981-82 in western Montana. Calls given to the initial appearance of the predator did not differ on the basis of predator type, but variations in call parameters were related to the alarm level. Higher alarm releases received a greater number of calls and these calls had a shorter length, a shorter interval between successive calls, and a higher proportion of calls with secondary frequencies (harsh calls). Playback experiments confirmed that the number of calls affected the alert response with 3 or more calls receiving a higher alert response than 1 or 2 calls. The degree of harshness of individual calls did not affect alert response.

Calls given repetitively, after the predator had been seen and initial calls given, differed on the basis of predator type. Hollow chirps were given to raptors and shrill/harsh chirps to dogs. Calls continued at regular intervals of about 2 seconds for up to 30 minutes or more. No differences in alert response to these two call types were noted during playback experiments but other evidence suggests that hollow chirps may indicate less alarm than shrill/harsh chirps.

The reasons for use of a call system that differs on the basis of predator type versus one that doesn't are discussed, as is the functional significance of alarm calls by Columbian ground squirrels in particular, and alarm calling in general in the family Sciuridae.

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Introduction

Vocalizations in response to predators, referred to as alarm or anti-predator calls, are widespread among animals. A large body of research has concentrated on both the function of these vocalizations and the information contained in them.

Among mammals, the most rigorously studied group is the primates. However, during the past 15 years, considerable attention has focused on the family Sciuridae, in particular the ground dwelling species. Some of the emphasis has been on the evolution of alarm calls and the role of kin selection (eg. Sherman 1977; Dunford 1977; Schwagmeyer 1981; Davis (in press)). Other researchers have examined the communication aspect of alarm calling, specifically, what information is conveyed by these calls. Experimental releases of simulated predators and the use of playback experiments have added to the information gathered from field observations (Turner 1973; Owings and Virginia 1978; Robinson 1981; Leger et al. 1980; Harris et al. 1983).

A number of theories have been presented regarding the function of alarm calls (eg. manipulation of conspecifics (Charnov and Krebs 1979); discouragement of predator pursuit (Dawkins and Krebs 1978)). However, the major function of alarm calls in the family Sciuridae appears to be aiding conspecifics in avoiding capture during predator encounters (Sherman 1977). The minimum information contained in the calls would be that danger is present. However, additional information may be conveyed, such as the type of danger (Davis (in press)), the alarm level associated with the alarm situation (Robinson 1981), or the appropriate defensive behavior (Owings and Virginia 1978; Leger et al. 1980; Leger and Owings 1978).

Some sciurid species give different calls to aerial and terrestrial predators (eg. S. beecheyi (Owings and Virginia 1978); S. richardsoni (Davis (in press)); S. parryi (Melchior 1971)) while others do not (eg. S. tridecemlineatus (Schwagmeyer 1980); Marmota caligata (Taulman 1973); Cynomys ludovicianus (Waring 1970)). The reasons for this difference are unknown, but it seems likely that the system used is a reflection of predator pressures. Species

that use a different behavioral response depending on the predator type would be expected to give different calls to these predators whereas species that use the same response regardless of predator type would not (Marler 1977). Detailed examination of a variety of species and calling systems may help in understanding the information conveyed by alarm calls and the reasons for the evolution of different defensive strategies.

Columbian ground squirrels (*S. columbianus*) have been observed during field studies and appear not to use a different call to aerial versus terrestrial predators (Betts 1976). Playback studies have indicated that some variations in call characteristics are related to alarm level, suggesting that the urgency of escape may be specified in their alarm calls (Harris et al. 1983).

In order to examine the information content of Columbian ground squirrel alarm calls, I conducted a series of predator release experiments and varied both the predator type (raptor versus dog) and the alarm level of the release. The results are presented in three papers:

1. The alarm calls given in response to the initial appearance of trained raptors and dogs.
2. Repetitive calls given after the release of trained raptors and dogs.
3. The responses of squirrels to playback of variations in call parameters recorded to the initial appearance of trained raptors and dogs.

The information obtained from these experiments provide some insights into the function of alarm calls in Columbian ground squirrels, and possibly, in other ground dwelling sciurid species.

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**I. Paper 1. Alarm Vocalizations of the Columbian Ground Squirrel (Spermophilus columbianus)
in Response to the Initial Release of Trained Raptors and Dogs**

A. Abstract

Alarm vocalizations of Columbian ground squirrels (Spermophilus columbianus) were recorded to the initial appearance of trained raptors and dogs. The calls did not differ on the basis of predator type but varied with the level of alarm associated with the release. Higher alarm releases received a greater number of calls, a greater proportion of calls with secondary frequencies (harsh), and calls were shorter in length and were separated by shorter intervals. The use of a non-predator differentiated alarm call system likely reflects the similarity in escape response appropriate to aerial and terrestrial predators.

B. Introduction

Vocalizations in response to predators have been documented for a large number of sciurid species. In particular, studies have been conducted to determine what information, if any, is conveyed to conspecifics by alarm calls.

It seems probable that all sciurid alarm calls warn conspecifics of danger (Sherman 1977). In addition, calls may also convey information about the defensive behavior appropriate during predator encounters (Owings and Virginia 1978; Leger et al. 1980). Calls can be further separated into two general categories; those that differ depending on the predator type, and those that don't. One would expect that species employing different defensive strategies that depend on the kind of predator might evolve a system of alarm calling such that different calls are given to different predators (Marler 1977). Conversely, species that give different alarm calls to different predators might employ different escape behaviors to these predators. This seems to be the case with Beechey ground squirrels (*S. beecheyi*) (Owings and Virginia 1978), Richardson's ground squirrels (*S. richardsoni*) (Davis (in press)) and Vervet monkeys (*Cercopithecus aethiops*) (Seyfarth and Cheney 1980). On the other hand, an alarm call system that does not differ according to the kind of predator would be likely in species that have the same escape response regardless of predator type.

Sciurids can be grouped loosely into three categories with regard to predator differentiation in their calling systems. The most highly predator-differentiated species usually give structurally different calls in response to aerial and terrestrial predators (although few, if any, appear to truly specify predator type (Owings and Hennessy (in press); Balph and Balph 1966; Robinson 1981)). Species classified as intermediate in differentiation tend to give different calls to aerial versus terrestrial predators, but the degree of overlap is high. In the third group, calls vary little toward different predators. In all three groups, variability of calls is likely related to alarm level and this is probably the most important information conveyed (Robinson 1981). (See Table 1 for a summary of species in these three categories).

Many studies of alarm calls have relied largely on naturally occurring predator attacks. While this method has the advantage of being realistic, it does not allow any control over the attack situation. Other workers have used an experimental approach with a variety of terrestrial stimuli (Owings and Virginia 1978; Davis (in press); Cherry 1979; Schwagmeyer 1980) and one used trained raptors to represent aerial predators (Turner 1973). In all previous work on calling, no attempt was made to control the degree of alarm associated with the appearance of the predator.

Columbian ground squirrels (*S. columbianus*) are known to give alarm calls during predator encounters and these vary structurally (Betts 1976; Harris et al. 1983). Furthermore, Columbian ground squirrels respond differently depending on the call broadcast during playback experiments (Harris et al. 1983), suggesting that information is transmitted. However, calls of Columbian ground squirrels in response to different types of predators or to varying degrees of alarm have not been investigated.

I conducted experimental releases of trained raptors and dogs, varying both the predator type and the alarm level of releases, to determine the extent of predator and alarm differentiation in the calling system of Columbian ground squirrels.

C. Methods

Experiments were conducted in nineteen Columbian ground squirrel colonies on a five thousand acre cattle ranch (46° 35' N, 114° 5' W, elevation 1000m) 10 kilometres northwest of Stevensville, Montana from 24 May to 18 June, 1981, and from 4 to 20 June, 1982.

Observations and recordings were made using blinds and natural cover. A trained male red-tailed hawk was used for 72 aerial trials and a female prairie falcon was flown during 10 trials. Nylon fishing line in a fishing reel was attached to the jessup of the birds to prevent their escape. Sixty-five trials with a terrestrial predator were conducted using a three-year-old black Labrador retriever. An average of 7.5 trials was conducted on each colony with a mean of 1.2 days between subsequent trials on the same area. There were no significant differences

between raptor and dog trials in terms of the distance from the release site to the colony (average of 62 m for raptors, 52 m for dogs), the time between successive trials on the same area, and the pre-trial behavior of the squirrels (Appendix 1).

I usually waited until squirrels were engaged in a non-alert type of activity such as grooming, feeding, or basking before releasing the predator. The raptor flew rapidly at an average height of 8 m (range, 2-12 m) and for an average distance of 70 m (range, 15-120 m). It usually flew either directly over the squirrels or landed on or at the edge of the colony, remaining motionless on the ground until retrieved between one and four minutes later.

Two types of dog trials were conducted. In Fast Dog trials, the dog ran rapidly towards the colony after being released from the blind area. He usually ran through the colony area, occasionally stopping at burrow entrances, and returned to the blind after a few minutes either on his own initiative or after being summoned vocally. Slow Dog trials were conducted from a truck parked along the road at the edge of accessible colonies. When squirrels were behaving in a non-alert manner the dog was carefully let out of the side of the truck furthest away from the colony. The dog trotted slowly along the road staying close to the truck, and after a minute or two was summoned back and let into the truck again.

Calls during Raptor and Fast Dog trials were recorded using a Uher 4000 Report Monitor tape recorder with a Sony AKG 1000 microphone and a Grampian parabola. Tape speed was 9.5 cm/s. Slow Dog trials were recorded using a Nagra IV tape recorder with a Sennheuser MKH 105 microphone at a tape speed of 19 cm/s. Sony P.R. 150-5 tape was used for all recordings. The tape recorder was turned on before a release and recording continued at least until the stimulus was retrieved (raptor) or back in the blind (dog) and usually longer.

A Kay Elemetrics Co. Digital Sonograph 7800 with Sonagraph Printer 7900 was used for structural analysis. Whenever possible, Power Spectrums (sections) were made of all calls having more than one frequency component in order to measure relative intensity of the components. These were used to compute the 'harshness' of a call (a score combining the relative intensity (in decibels) and the number of secondary components).

Based on the results of my experiments, trials were separated into two phases. The release phase included the initial reactions of the squirrels to the appearance of the predator. This was usually followed by a short pause, then a repetitive phase. Repetitive calls were given at regular intervals of about two seconds for up to an hour or more. Repetitive calls to raptors were structurally distinct from release calls making it easy to distinguish between the two phases, but repetitive calls to dogs were similar to release calls and it was not always possible to determine when the repetitive phase began. Thus, only the first 5 seconds of calling were used for analyses. All but 1% of release calls to raptors and approximately 11% to dogs occurred within the first 5 seconds. This paper is concerned with the release phase only (see Lickley 1984 for an analysis of repetitive calling).

The following call parameters were measured and compared; frequency, frequency modulation, and length of the dominant component, the harshness of the call, the number of double calls (two calls given so close together that they are joined (Figure 1c), the number of multiple calls (3 or more calls given in rapid succession resulting in a chatter sound)(Figure 1d), the total number of calls, and the interval between successive calls. Harshness was measured in three ways: the average harsh score per harsh call during a trial, the maximum harsh score per trial, and the proportion of calls having harsh components during each trial.

All analyses were done using individual squirrels that were recorded during a trial. Comparisons between stimulus situations were done on a per trial basis with one squirrel used per trial. During the few trials where calls of more than one squirrel could be distinguished, the squirrel giving the higher number of calls was used.

Behavioral responses of up to 5 squirrels per trial were monitored during Raptor and Fast Dog trials but not during Slow Dog trials. Responses measured included first behavior, the direction faced by the squirrels immediately after release of the stimulus, and whether or not a squirrel called during the release phase. First behavior was ranked on the basis of level of alarm and classified as 1 = no reaction, 2 = little reaction (turned or assumed a sitting posture), 3 = alert posture (vertical or horizontal alert), 4 = ran to a mound and assumed an alert posture,

and 5= ran to a mound and went partially or completely into the burrow.

Mann-Whitney tests were used for each call variable for comparisons between stimuli. Discriminant function analyses (Nie et al. 1975) were used to test the degree of separation between stimulus situations based on a combination of call parameters. Chi square and Spearman's Rank Correlation tests were used to compare behavioral responses and to compare these responses to variations in call parameters. For all statistical analyses, a probability level of 0.05 or less was considered significant.

D. Results

One hundred and forty-seven trials were conducted but only 80 were used for analyses. Trials not used included those with no audible calls, those in which calls were not analyzable owing to excessive background noise or faintness of the call, and those in which more than one squirrel called simultaneously making it impossible to distinguish individual squirrels.

The basic alarm chirp used by Columbian ground squirrels during my predator release experiments was the shrill chirp (Figure 1a)(see Harris et al. (1983) for terminology). This chirp had an average dominant frequency of 59 kHz (range, 51 to 65 kHz) and an average length of 61 ms (range, 45 to 120 ms)(Table 2). The most obvious variation was the presence of secondary components not related to the dominant component in some chirps. These calls (=harsh shrill chirps (Harris et al. 1983)) varied in number and intensity of secondary components (Figure 1b). An average of 45% of calls were harsh shrill chirps.

Comparisons of Raptor versus Slow Dog, and Fast Dog versus Slow Dog trials show similar differences in call parameters. Slow Dog trials received significantly fewer double, multiple, and total calls as well as fewer harsh shrill calls (Table 2). Also, the length of calls was greater in Slow Dog trials (Table 2). The interval between successive calls was significantly shorter to Raptor versus Slow Dog, but not to Fast versus Slow Dog trials, and frequency was significantly lower in Fast versus Slow Dog trials, but not in Raptor versus Slow Dog trials (Table 2). Frequency modulation, average harshness, and maximum harshness were not

significantly different between trial types (Table 2).

There were no significant differences between Raptor and Fast Dog trials in any of the parameters measured, but Fast Dog trials were consistently intermediate in value between Raptors and Slow Dog trials in the parameters mentioned above (Table 2).

Discriminant function analyses indicate a relatively low discrimination between Raptor versus Slow Dog, and Fast Dog versus Slow Dog trials, and an even lower discrimination between Raptor versus Fast Dog, and Raptor versus All Dog trials (Table 3).

The behavioral responses of squirrels to predator releases varied from no change in behavior to immediately running down a burrow. The mean rank of the first behavior after release was the same for Raptors and Fast Dogs (3.6) but first behavior was significantly higher to Raptor releases based on a Mann-Whitney comparison (Table 4). Also, more squirrels ran immediately and more went down burrows to Raptor releases (Table 5). In addition, more squirrels ran if they were not alert prior to release regardless of the predator type (Appendix 1).

Squirrels tended to orient immediately toward the predator rather than toward the caller during both Raptor and Fast Dog trials, but more so in Fast Dog trials (51% versus 92% respectively (Table 5).

Fewer squirrels called during Raptor trials than during Fast Dog trials (Table 5). Since squirrels usually stayed up longer to dog trials and only went down when the dog was close, they had more opportunity to call to dogs.

The number of calls was significantly correlated with all parameters except frequency and frequency modulation (Table 6). In addition, interval was correlated with length and average harshness was correlated with proportion of calls that were harsh (Table 6). No significant correlations with any call parameters were found for running, going down burrows, or in first behavior (Table 6).

In an attempt to find some measure of the effect of the calls on the squirrels and thus of the alarm level of a trial, I compared trials where non-alert squirrels immediately ran (high

alarm) versus trials where first behavior did not involve running (low alarm). I eliminated all squirrels that called during a trial on the grounds that they may have been responding to the predator rather than the calls. Once these squirrels were matched to trials with analyzable calls, only 8 running (high alarm) and 7 non-running (low alarm) trials were available for analysis. Mann-Whitney tests revealed no differences between these groups in any of the call parameters (Table 4).

E. Discussion

The results of my predator release experiments clearly indicate that information regarding the type of predator is not transmitted to conspecifics by the alarm calls of Columbian ground squirrels. None of the nine call parameters measured differed significantly between Raptor and Fast Dog trials. Instead, alarm level appears to be the main information contained in the calls. Slow Dog trials represented a low alarm situation, while Raptor and Fast Dog trials represented a higher alarm, although there was a gradient of alarm level in the Raptor and Fast Dog releases varying from extreme to low alarm depending on the circumstances of the trials. Fast Dog trials were probably less alarming than Raptor trials since the speed of the raptor was greater and the time it took to reach the colony shorter. This is suggested by the fact that Fast Dog trials had mean values intermediate between Raptor and Slow Dog trials for all significant parameters.

Of the nine parameters measured, four were significantly different between Raptor and Slow Dog, and between Fast and Slow Dog trials. The greatest difference was in the number of calls given; Slow Dog trials received fewer calls than any of the other release situations. This is unlike the trends for some other sciurids (eg. *S. beldingi* (Robinson 1981); *S. parryi* (Melchior 1971)) in which high alarm situations are associated with a small number of calls, but is similar to the reactions of *S. beecheyi* to terrestrial predators (Owings and Virginia 1978). In Columbian ground squirrels it seems reasonable that a higher number of calls indicates a higher alarm level since squirrels that remain above ground and call to predators might experience high

excitation rates and thus continue calling while the predator is in view. On the other hand, in an extreme alarm situation (which probably rarely occurred during my predator releases) it seems likely that a squirrel would only have time to emit a few calls prior to escaping down a burrow (Leger et al. 1980). In that situation, it may be that other call parameters serve to convey levels of alarm to neighboring Columbian ground squirrels.

One of these parameters could be the length of the call since Raptor and Fast Dog trials (high alarm) received shorter calls than Slow Dog trials (low alarm). Other sciurids may use length in a similar manner to convey alarm level (eg. M. caligata (Taulman 1977); M. vancouverensis (Heard 1977); S. beldingi (Robinson 1981); S. beecheyi (Owings and Virginia 1978); and S. richardsoni (Davis (in press))). It seems plausible that during high alarm situations, calls would be shorter in length, allowing calling squirrels more time to escape.

A third parameter that seems related to alarm level is the interval between successive calls. Calls during Raptor trials had a much shorter interval than during Slow Dog trials. No difference was found between Slow Dog and Fast Dog trials, but that was likely a reflection of the small Slow Dog sample size for this parameter (50% of Slow Dog trials received only one call and therefore had no interval measurement). A shorter interval was postulated to be an indicator of high alarm in Columbian ground squirrels by Betts (1976). A short interval between calls is also associated with higher alarm level in many other sciurids (eg. M. flaviventris (Waring 1966); Cynomys (3 species) (Waring 1970); S. tridecemlineatus (Schwagmeyer 1981); S. beldingi (Robinson 1981); and S. beecheyi (Owings and Virginia 1978)).

Interval seems a likely parameter to use for urgency during many alarm situations as it would reflect excitation of the caller without compromising the time needed for escape. However, during extreme alarm situations, squirrels may not have time for more one or two calls and interval would not be useful as an indicator of alarm. A shortened interval coupled with a higher number of calls likely is related to the increased number of double and multiple calls during Raptor and Fast Dog releases.

A parameter that also seems a likely candidate as an indicator of alarm level is the degree of harshness of the call. Harsher calls were found to be more alarming in S. beecheyi (Owings and Virginia 1978), as well as during previous playback experiments with Columbian ground squirrels (Harris et al. 1983). However, harshness does not seem to be used as an indicator of alarm in most other sciurids.

During my predator release experiments there was a difference in the proportion of harsh shrill versus pure shrill chirps given during a trial; higher alarm trials received more harsh shrill chirps. Therefore, it seems probable that the number of harsh shrill chirps is used to some degree as an indicator of alarm. However, the degree of harshness of individual calls did not seem to reflect the level of alarm since neither the maximum harshness of calls, nor the average harshness per harsh call differed between Raptor and Fast Dog versus Slow Dog trials.

Betts (1976) postulated that higher frequencies reflected higher levels of alarm in Columbian ground squirrels, and frequency has been similarly mentioned as an indicator of alarm in S. beldingi (Robinson 1981); S. armatus (Balph and Balph 1966), and S. tridecemlineatus (Schwagmeyer 1981), but not in S. beecheyi (Owings and Virginia 1978), and Marmota flaviventris, M. caligata and M. vancouverensis (Waring 1966; Taulman 1977; Heard 1977). During my experiments, frequency was significantly different between Fast and Slow Dog trials but in the opposite direction predicted by Betts (1976). In addition, no difference was found between Raptor and Slow Dog trials. It seems probable that frequency does not indicate the level of alarm in Columbian ground squirrels and the reason for the difference between Fast and Slow Dog trials may have been the small sample size of Slow Dog trials.

Frequency modulation was found to be an indicator of alarm in S. beecheyi (Owings and Virginia 1978), and of predator type and/or alarm in S. richardsoni (Davis (in press)) but was not found to be an indicator of alarm in Columbian ground squirrels. In addition, the intensity of the call was postulated as being an indicator of alarm in some sciurids (eg. M. vancouverensis (Heard 1977); various tree squirrels (C.C. Smith 1980; Emmons 1978)). It seems probable that louder calls reflect higher excitation and alarm levels in Columbian ground

squirrels, but I was not able to measure intensity.

Although several characteristics of calls correlated with the intensity of alarm during my predator releases, a combination of these parameters did not clearly discriminate between high and low alarm trials. The reason for this is not apparent, but may be a result of the small sample size of low alarm trials and the gradient of alarm levels that existed in the high alarm trials.

The behavioral information collected during release experiments could be used in some cases to calculate the alarm level associated with a particular trial. However, a number of complicating factors may influence those data. For instance, first behavior was found to be negatively correlated with the distance from the release site to the colony. Also, the behavior prior to release, especially whether or not a squirrel was alert or not, influenced the tendency to run immediately after release.

First behavior was significantly higher to Raptor than to Fast Dog trials, and more squirrels both ran and entered burrows during Raptor trials. Davis (in press) also reported that Richardson's ground squirrels ran immediately more often to aerial versus terrestrial predators calls, and Leger et al. (1977) found that Beechey ground squirrels both ran more often and assumed a lower alert posture to aerial than to terrestrial predator calls. They postulated that responses may have been related to the different hunting styles of these two predator types. In my experiments, differential running likely reflected a higher alarm level associated with aerial releases rather than a different response to aerial versus terrestrial predators since there was a considerable degree of overlap in behavioral responses to the two types of predators.

As was found in vervet monkeys (Seyfarth and Cheney 1980), squirrels were more likely to look toward the predator rather than the caller upon hearing an alarm call. This was especially apparent in Fast Dog trials where only 7% of the squirrels faced in the direction of the caller, versus 21% during Raptor trials. Searching immediately for the source of alarm rather than the caller would seem to be a more reliable way to obtain information and assess the danger. In addition, the peripheral vision of squirrels may allow them to watch the caller

while they search for the predator during many predator encounters. However, the quick reactions of squirrels during my predator releases made it difficult to determine whether this occurred.

In summary, Columbian ground squirrels do not give calls that specify the type of predator during the release phase of predator encounters. Instead, they appear to convey information regarding the level of alarm associated with the predator encounter. The major indicators of alarm are the number of calls, the interval between successive calls, the length of the call, and the proportion of harsh to shrill calls. Based on these results, it appears that the multiple harsh chatter (combining number of calls, length of calls, and interval between successive calls) represents the highest alarm level in Columbian ground squirrels, at least in the Montana populations studied. This may not be true of some Alberta populations as multiple chatters are rarely heard there even during situations of extreme alarm (W. King, J. Murie, M. Harris (pers. comm.)):

The use of a non-predator differentiated system is consistent with Marler's hypothesis. He postulated that species that use different responses depending on the predator type might be expected to give different calls to these predators (Marler 1977). Field observations indicate that Columbians are not selective in their choice of burrows to enter (unlike S. beldingi (Turner 1973). Rather, they seek refuge in the nearest burrow during all predator encounters (unpubl. data). Also, there is no indication that squirrels behave in any consistently different manner while escaping aerial versus terrestrial predators based on my experimental data.

Fewer defensive strategies are likely needed for the habitat and predator pressures experienced by Columbian ground squirrels in my study area compared to S. beecheyi (Owings and Coss 1977; Owings and Virginia 1978). However, Columbian ground squirrels appear to have similar predator pressures as S. richardsoni. Thus, it seems puzzling that the two species differ in their alarm call systems. One possible explanation is that the wooded, generally hilly habitat of Columbian ground squirrels may offer more cover for predators and allow them to get closer to a colony undetected than does the open prairie habitat of S. richardsoni. If both

aerial and terrestrial predators hunt Columbian ground squirrels largely by stealth, the same escape behaviors may usually be appropriate for both types of predator; hence there would be no reason for calls to the two predator types to differ. Field observations indicate that both goshawks and coyotes use cover to catch squirrels by surprise (W. King (pers. comm.); M. Harris (pers. comm.)). However, it is not known to what extent Red-tailed hawks rely on either stealth or cover when hunting Columbian ground squirrels. The extent of similarity in hunting techniques and threats posed by aerial versus terrestrial predators has not been well documented for any sciurid, including Columbian ground squirrels. This is an important area for future study. In addition, playback experiments of the effects of variations in call parameters are necessary in order to verify the relationship between call parameters and alarm level in Columbian ground squirrels.

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Table 1. Classification of alarm call systems in the family Sciuridae on the basis of highly predator differentiated, intermediate, and non-predator differentiated call types, and parameters of calls that vary. (no=number of calls, lth=length, int=interval between calls, har=harshness, freq=frequency, freq mod=frequency modulation, inty=intensity)

System	Parameters	Source
Predator Differentiated		
<u>Spermophilus beecheyi</u>	no, lth, int, Owings & Virginia 78 har, freq mod Leger & Owings 78	
<u>Spermophilus undulatus</u>	no, har	Melchoir 71
<u>Spermophilus armatus</u>	no, freq	Balph & Balph 66
<u>Spermophilus richardsoni</u>	lth, freq mod	Davis (in press)
Intermediate		
<u>Marmota caligata</u>	lth	Taulman 77
<u>Marmota vancouverensis</u>	lth, inty	Heard 77
<u>Spermophilus beldingi</u>	lth, no, freq	Robinson 81
Non-predator differentiated		
<u>Marmota flaviventris</u>	int	Waring 66
<u>Citellus tridecemlineatus</u>	freq, int	Schwagmeyer 80
<u>Cynomys ludovicianus</u>	int, lth,	Waring 70
<u>C. leucurus</u> & <u>C. gunnisoni</u>		Fitzgerald et al. 74
<u>Tamiasciurus hudsonicus</u>	int, inty	Smith 78
<u>Spermophilus columbianus</u>	int, freq, har	Betts 76 Harris et al. 76
African Rainforest Species	lth, inty	Emmons 78

Table 2. Comparisons of parameters measured (on a per trial basis) of calls given by Columbian ground squirrels to Raptor, Fast dog, and Slow Dog releases. Means ($\pm$ S.E.) are listed and probabilities are based on Mann-Whitney tests (*= $p < 0.05$, **= $p < 0.01$, ***= $p < 0.001$) All comparisons between Raptor and Fast Dog trials had a $p > 0.05$.

Parameter	Raptor			vs.		Slow Dog			vs.		Fast Dog		
	N	Mean			p	N	Mean			p	N	Mean	
Number of Call	38	9.2	± 1.0	***		10	1.9	± 1.2	***		32	7.3	± 4.8
Number of Double Calls	35	2.8	± 0.3	***		10	0.4	± 0.3	***		31	2.5	± 0.3
Number of Multiple Calls	35	1.2	± 0.2	**		10	0.0	± 0.0	**		32	0.8	± 0.3
Interval between Calls (ms)	36	189	± 22.7	*		5	1238	± 651.8			28	331	± 69.1
Length (ms)	30	59	± 2.2	**		10	78	± 6.2	*		29	61	± 2.8
Frequency (kHz)	37	5.7	± 0.7			10	6.1	± 1.3	*		30	5.7	± 0.9
Frequency Modulation (kHz)	19	1.5	± 0.0			8	1.4	± 0.0			16	1.5	± 0.0
Average Harsh	30	23.8	± 4.0			10	9.8	± 5.2			27	18.1	± 4.2
Maximum Harsh	30	28.1	± 4.7			10	10.6	± 5.7			27	21.9	± 5.3
% Harsh Calls	31	55.9	± 8.4	**		10	10.0	± 6.7	*		32	45.9	± 8.2

Table 3. Discriminant Function Analysis (Method=Direct)
between Raptor (n=34) and Fast Dog (n=30), Raptor and Slow
Dog (n=10), Raptor and All Dog, and Fast and Slow Dog
trials on the basis of call parameters. Percent predicted
group membership, percent correctly classified, and
parameters used in function are given.

	Group Number	%Predicted Group		%Correctly Classified	Parameters Used
		1	2		
Raptor	1	55.9	44.1	57.8	Avg. Harsh
&					Interval
Fast Dog	2	40.0	60.0		
Raptor	1	85.3	14.7	72.7	Frequency
&					Avg. Harsh
Slow Dog	2	70.0	30.0		
Raptor	1	55.9	44.1	58.1	Interval
&					%Harsh calls
All Dog	2	40.0	60.0		Frequency
Fast Dog	1	13.3	86.7	67.5	Avg. Harsh
&					Length
Slow Dog	2	10.0	90.0		Frequency

Table 4. a) First behavior (ranked from 1=lowest alarm to 5=highest alarm) during Raptor and Fast Dog trials, and b) number of calls, length of calls, interval between calls, and proportion of harsh calls, during high alarm (squirrels ran) and low alarm (squirrels did not run) trials. Means and standard errors are given. Probability values are based on Mann-Whitney tests.

	Raptor (N=207)		Fast Dog (N=67)		M-W
	Mean	S.E.	Mean	S.E.	
a) First Behavior	3.9	.08	3.6	.09	p<0.05
	Ran (N=8)		Didn't Run (N=6)		
	Mean	S.E.	Mean	S.E.	
b) Number of Calls	8.5	2.5	8.5	0.6	p>0.9
Interval (ms)	164	42.0	281	61.2	p>0.1
Length (ms)	54	2.5	59	4.9	p>0.4
% Harsh	67.3	17.5	67.0	20.9	p>0.9

Table 5. Behavioral responses (% squirrels that ran, entered burrows, faced predator initially, and called) to Raptor and Fast Dog releases.

	Raptor		Dog		χ^2 X
	(N)	%	(N)	%	
Ran	(90)	59	(48)	40	$p < 0.05$
Down Burrow	(90)	43	(48)	19	$p < 0.01$
Faced Predator	(76)	51	(89)	92	$p < 0.001$
Called	(171)	12	(34)	71	$p < 0.001$

Table 6. Spearman's Rank Correlations between five call parameters during the release of trained raptors and dogs, and between these parameters and first behavior of squirrels. Only call parameters that were significantly correlated are listed.

	Number of Trials	Correlation Coefficient	Probability
1. Number of Calls			
versus			
a) Interval	62	-0.34	<0.01
b) Length	59	-0.66	<0.001
c) Average Harshness	54	0.32	<0.01
d) Proportion Harsh	60	0.22	<0.05
2. Interval			
versus	57	0.49	<0.001
Length			
3. Average Harshness			
versus	54	0.85	<0.001
Proportion Harsh			
4. First Behavior			
versus			
a) Number of Calls	64	-0.09	>0.2
b) Interval	62	-0.05	>0.3
c) Length	59	0.06	>0.3
d) Average Harshness	54	0.10	>0.2
e) Proportion Harsh	60	0.12	>0.2

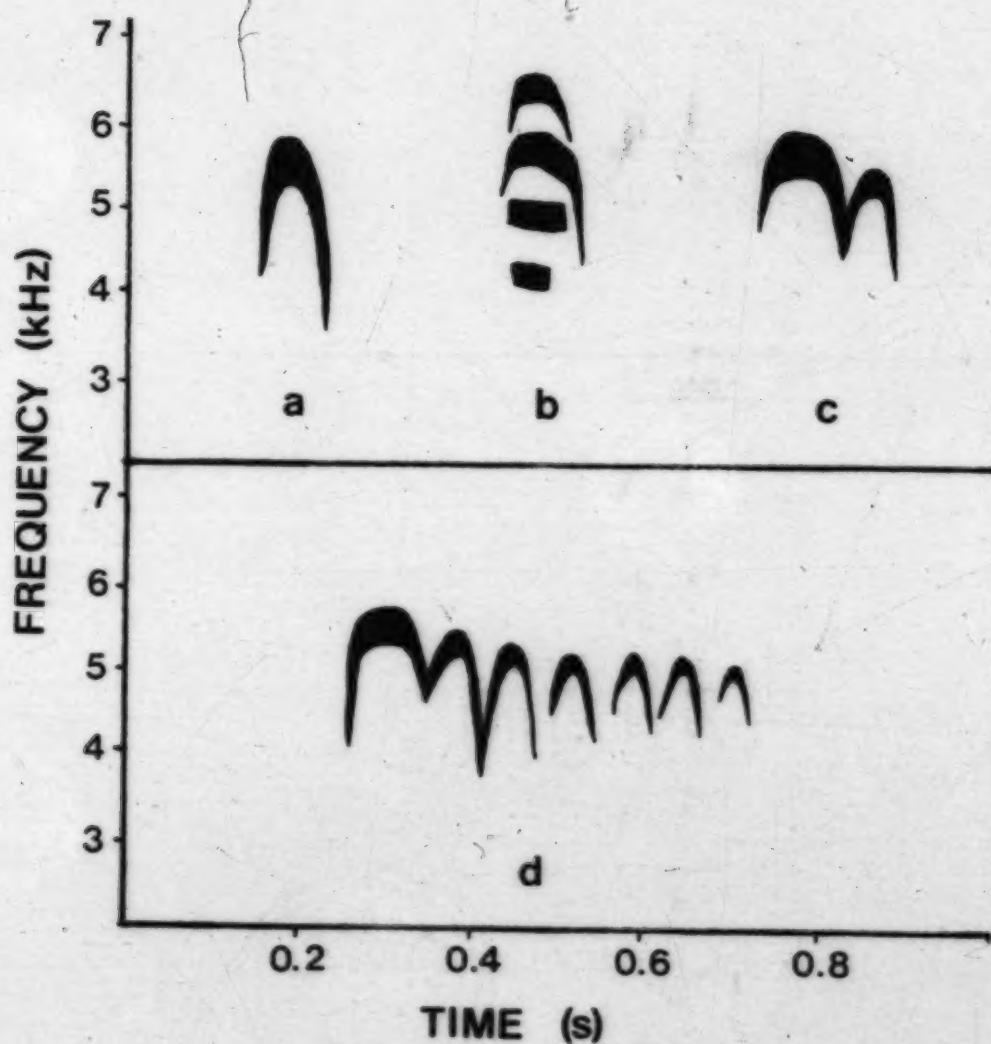


Figure 1. Representative sonograms (wide band) of calls given by Columbian ground squirrels in response to the release of trained Raptors and Dogs. (a= shrill, b= harsh shrill, c= double shrill, d= multiple shrill).

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II. Paper 2. Repetitive Vocalizations of the Columbian Ground Squirrel (Spermophilus columbianus) in Response to Predators

A. Abstract

Repetitive vocalizations given by Columbian ground squirrels (Spermophilus columbianus) after the release of trained raptors and dogs were studied during the summers of 1981-82 in western Montana. These calls began after the predator had been seen and initial alarm calls given, and continued at regular intervals of about 2 seconds for up to an hour or more. Hollow chirps were given to raptors and shrill/harsh chirps to dogs. Playback experiments revealed no differences in the alert responses of squirrels to these 2 call types. The probable function of these repetitive calls is to monitor predator movements and maintain vigilance. The use of a different repetitive call to aerial and terrestrial predators may be due to the different threats posed by these two predator types during the repetitive phase with aerial predators representing a lower threat.

B. Introduction

The focus of most studies of alarm vocalizations in the family Sciuridae has been on calls given during the initial appearance or attack of a predator. However, Betts (1976) and Owings & Hennessy (in press) mentioned another class of calls that begin after the initial alarm calls and continue at relatively constant intervals for up to an hour or more.

Owings and Hennessy suggested that repetitive calls should be treated as functionally distinct from calls given during the initial predator attack. It has been postulated that repetitive calls serve to maintain vigilance and to communicate information about the predator's movements and location (Melchior 1971; Morton and Shalter 1977; Byrne 1981; Owings and Hennessy (in press)). In addition, they may lower the response threshold, thus decreasing the reaction time during subsequent predator attacks. However, there has been little study of this phase of interactions with predators and the functional significance of repetitive calls remains

hypothetical.

In S. beldingi and S. beecheyi repetitive calls are structurally similar to initial alarm calls (Robinson 1981; Owings et al. 1977), whereas in Marmota vancouverensis and S. columbianus repetitive calls are structurally different (Heard 1977; Betts 1976). In most sciurids only one repetitive call is used and no mention has been made of a different call for aerial versus terrestrial predators (Table 1).

Repetitive calls were frequently recorded during my investigation of alarm vocalizations given by Columbian ground squirrels in response to trained raptors and dogs. Data on these calls are presented here, as well as the results of playback experiments to assess behavioral responses to them. The functional significance of repetitive alarm calling in the Columbian ground squirrel is explored.

C. Methods

1. Predator release experiments

Predator release experiments were conducted on a 2,000 ha. cattle ranch (46° 35' N, 114° 5' W, elevation 1000m) 10 kilometres northwest of Stevensville, Montana from 24 May to 18 June, 1981, and from 4 to 20 June, 1982. A trained male red-tailed hawk was used for 72 aerial predator trials and a female prairie falcon was flown during 10 trials. The raptor usually landed on or near the colony and remained motionless until retrieved. Sixty-five terrestrial predator trials were conducted using a three year old black Labrador retriever. Two types of dog trials were run. In Fast Dog trials the dog ran at and through the colony and returned to the blind after a few minutes, either on its own initiative or after being summoned vocally. In Slow Dog trials the dog was visible to the squirrels, but stayed near the blind and did not enter the colony (see Lickley (1984a)).

A tape recorder was turned on prior to a release and recordings continued at least until the stimulus was retrieved (raptor) or back in the blind (dog) and usually longer. Thus a representative sample of repetitive calls was recorded during each trial. The calls were then

monitored by ear for a number of minutes after the recorder was turned off.

A Kay Elemetrics Co. Digital Sonograph 7800 with Sona Graph Printer 7900 was used for structural analysis of recorded calls and a sound-pulse timer was used to measure the interval between calls.

Two phases of calling were distinguished. The release phase included the first five seconds of calls given immediately after the predators' release. The repetitive phase included calls after five seconds, but was further broken down into calls while the predator was moving and calls while the predator was either not moving or not visible to calling squirrels. Only the latter were used for comparisons between raptors and dogs and between call types.

Comparisons between calls were made using Mann-Whitney U tests.

2. Playback Experiments

Playback experiments were conducted from 4 to 19 July 1982 in the Highwood River drainage 46 km west of Longview, Alberta (50° 23' N, 114° 39' W, elevation 1500m) (see Lickley (1984b) for methods). The calls played were a series of five rapid shrill chirps recorded during the release phase of a Fast Dog trial, followed by a 3 second pause and then 20 seconds of either repetitive hollow or shrill chirps spaced 2 seconds apart (see below, Harris et al. 1983 for a description of calls). Playbacks were done on a paired basis; after the first call was played and squirrels resumed previous activities, the second call was played. The sequence of calls within a trial was alternated.

The type of posture and the time spent alert were compared using a paired Wilcoxon signed rank test. Alert postures were classified on the basis of alarm response as done by Harris et al. (1983) and Lickley (1984b). (0=no reaction, 1=head up, 2=slouch, 3=vertical, 4=vertical stretch, 5=partially in burrow). Time was measured from the beginning of alert activity until the squirrel resumed non-alert activity. Behavior was not monitored after non-alert activity resumed. An additional comparison was made, on an unpaired basis, between the series of five chirps only and the series followed by repetitive chirps using a Mann-Whitney test. A probability value of 0.05 or less was considered significant for all analyses.

D. Results

Call Types

Three different types of repetitive calls were recorded. Shrill chirps (see Harris et al. (1983) for terminology) were pure note vocalizations with no secondary components (Fig. 1b). They had a mean frequency of 5.5 kHz (range, 5.4-5.8 kHz) and a mean length of 63 milliseconds (range, 50-70 ms) (Table 2). Harsh shrill chirps had a dominant component similar in frequency and length to the shrill chirp, but contained one to five secondary components that were not multiples of the dominant component, giving a harsh or noisy quality to the sound. Shrill and harsh shrill chirps were similar to the alarm calls given during the initial appearance of a predator. Harsh shrill chirps were used as repetitive calls during only 8 of 61 trials analysed and were interspersed with shrill chirps. Therefore, shrill and harsh shrill chirps are combined for analyses.

Hollow chirps contained a dominant component with a mean frequency of 2.5 kHz (range, 2.0-2.8 kHz) and from zero to four related harmonics (Fig 1a). The mean length was 56 milliseconds (range, 30-90ms) (Table 2), and these calls had a rounder, fuller sound, easily distinguishable by ear from other alarm calls. Hollow chirps were never recorded during the release phase of a trial.

Alarm calls were recorded during the release phase of 52 percent and 66 percent of Raptor and Dog trials, respectively. These were followed by repetitive calls in 90 percent of Raptor and 60 percent of Dog trials.

Hollow chirps were associated with Raptor trials and shrill/harsh chirps with Dog trials. Seventy-nine per-cent of Raptor trials received hollow chirps only, fifteen per-cent received shrill/harsh chirps, and the remaining received both hollow and shrill/harsh chirps (Table 3). In contrast, all but one Dog trial received shrill/harsh chirps only; the remaining trial received 2 hollow and 75 shrill/harsh chirps (Table 3).

The interval between successive repetitive calls was significantly shorter for hollow chirps (1.9 s) than for shrill/harsh chirps (2.7) (Table 2). The interval for shrill/harsh calls

during Fast versus Slow Dog trials did not differ significantly, although the mean interval was slightly higher during Fast Dog trials (unpubl. data).

The interval between successive repetitive calls was relatively constant throughout a calling bout. This was in contrast to the more erratic intervals between successive shrill/harsh calls given while the dogs were still moving (Appendix 2). (No comparable measure of repetitive calls to moving predators was available for hollow chirps since raptors remained motionless after landing.)

Playback results

There were no significant differences in alert response to playback of repeated hollow versus repeated shrill chirps. Squirrels assumed a mean alert posture between vertical and slouch for both repetitive call types and stayed alert slightly longer to hollow than to shrill/harsh chirps (Table 4).

An unpaired comparison between the shrill series only and the shrill series plus repetitive calls revealed no significant differences in the time spent in alert posture (Table 4). Although the maximum alert posture indicated a higher alarm response to the repetitive calls, this posture was reached prior to the start of the repetitive portion of the playback and was not a result of the effects of repetitive calls (Table 4).

E. Discussion

1. Functional significance of repetitive calls.

When discussing functional significance of repetitive calling, two different categories should be distinguished; calls while predators are visible, and calls when predators are no longer visible.

In Columbian ground squirrels, (as in S. beecheyi (Owings and Hennessy (in press)) and M. flaviventris (Waring 1966)) repetitive calling while the predator is visible probably functions primarily to inform conspecifics about the predator's location since the rate of calling tends to increase when terrestrial predators increase speed or get closer to a calling

squirrel (Lickley (unpubl. data); M. Harris (pers. comm)). However, it is difficult to determine whether information concerning a predator's movements is being conveyed by the calls because non-calling squirrels may be responding to the predator rather than to the calls.

Byrne (1979) noted that vocalizations of Guinea baboons also change with the movements of some predators that hunt by stealth (eg. leopards) and he postulated that it would be functional to mark the location and comment on movements of predators that rely on an undetected close approach for hunting. However, this is not the case with predators that hunt in the open and rely on speed (eg. wild dogs). In the latter case, baboons simply watched the predator in silence from a safe position.

The predators of Columbian ground squirrels use both the undetected approach and speed from an exposed position when hunting (unpubl. data; J. Murie pers. comm.). However, unlike baboons, Columbian ground squirrels call in response to both hunting strategies (unpubl. data).

Repetitive calling may also function to discourage further attacks by informing the predator that at least one squirrel is vigilant (Owings and Hennessey (in press); Dawkins and Krebs 1978). This is also difficult to determine because discouraged predators are unlikely to be seen by an observer.

Repetitive calls could act as a deterrent against subsequent attacks by predators who hunt by stealth, but it does not seem to be an effective measure against predators who use speed from an exposed position when hunting (eg. S. armatus (Cherry 1979)). In fact, I have seen a coyote capture a squirrel while in full view of the colony and while repetitive chirps were going on. Thus, although some predators may be discouraged, others clearly are not.

Repetitive calling often continues after the predator has left the area and is no longer visible (Heard 1977; Waring 1970; Balph and Balph 1966; Brand 1976). These calls probably function primarily to maintain vigilance against subsequent attacks (Melchior 1971; Owings and Hennessey (in press)). Betts (1976) in fact, noted that Columbian ground squirrels seemed to look up more frequently during repetitive calling than when no calling occurred.

Owings and Hennessy (in press) postulated that repetitive calling may also serve to lower the threshold for response during subsequent attacks, thus decreasing the reaction time and increasing the squirrels' chances of escape. Maintenance of vigilance and/or lowering of response threshold would only be beneficial if there was some likelihood of a subsequent attack. To date, there are no published data to test this hypothesis. However, circumstantial evidence suggests that some raptors do return to a colony within a short period of time after an unsuccessful attack (W. King pers. comm.) and I have seen coyotes and badgers return to a colony several times after their initial departure.

Playback of recorded calls can be used to determine the response of squirrels in the absence of predators. In my playback experiments there was no significant difference in mean time spent alert and mean alert posture during repetitive calling compared to playback trials of the same release calls without repetitive calls. However, the comparison was not done on a paired basis and individual variation and other uncontrolled factors may have influenced the results. Also, no data were collected on subsequent vigilance or lowering of threshold response after non-alert behavior was resumed, and differences may only appear after a longer period of time. Finally, the period of repetitive calling that I used may have been too short to produce any differences in the squirrels' responses since my predator release data indicate that repetitive calls usually continued for a minimum of 3 minutes and increased vigilance and/or threshold lowering may only be affected after calls have continued for some time.

Harris et al. (1983) found that playback of repeated shrill chirps did not produce any differences in alert response when compared to playback of a single shrill chirp. Similarly, playback of repeated hollow chirps did not produce a difference in alert posture as compared to a single hollow chirp; however, squirrels spent a significantly longer time alert to the repeated hollow chirps. These observations suggest that repeated hollow chirps do increase vigilance whereas repeated shrill chirps have no obvious effect on the squirrels' behavior.

A number of problems arise in interpreting this information. Shrill chirps are used both during the release and repetitive phases of a predator interaction, but hollow chirps are only

given during the repetitive phase. Also, single hollow chirps may be used during social interactions, whereas shrill chirps are rarely used in such contexts (Harris et al. 1983). Thus, repeated shrill chirps may have no more effect on alert response than single shrill chirps because squirrels equate both with alarm situations. On the other hand, repeated hollow chirps may increase time spent alert because single chirps serve to produce attention rather than real alarm (Harris et al. 1983), whereas repeated chirps do elicit alarm reactions.

2. Functional significance of hollow versus shrill/harsh repetitive vocalizations.

Columbian ground squirrels are one of the few sciurids reported to have more than one type of repetitive vocalization and the only one with any degree of aerial-terrestrial separation in the use of repetitive calls. Hollow chirps were associated with aerial predators and shrill/harsh chirps with terrestrial predators. However, these two types of repetitive chirps are not completely predator specific since there was occasional overlap in their use and both are given occasionally to non-predatory mammals such as humans and ungulates (unpubl. data; Betts 1976).

The functional significance of having two repetitive alarm calls is difficult to assess with existing data, but different information could be extracted from the two calls. Possibilities include; alarm level, defensive behavior appropriate in response to subsequent attacks, likelihood of subsequent attack, or a combination of the above.

Ultimately, the purpose of all alarm calls is probably to warn conspecifics of danger (Sherman 1977), and possibly to convey information about the behavior that is most appropriate during predator encounters. Most species, including Columbian ground squirrels, appear to convey alarm level during the release phase, and in the case of Columbian ground squirrels it seems possible that the two repetitive calls represent different alarm levels.

One important indicator of alarm level during the release phase is the interval between successive calls, with shorter intervals associated with higher alarm levels (Robinson 1981; Lickley 1984a). During the repetitive phase hollow chirps had a shorter interval between calls than shrill/harsh chirps. Thus, hollow chirps could communicate a state of higher alarm than

do repeated shrill/harsh chirps.

However, Betts (1976) and Harris et al. (1983) both concluded that hollow chirps represented a lower level of alarm than shrill/harsh chirps because shrill/harsh chirps are used to indicate alarm during the release phase while hollow chirps are used more often during non-alarming social interactions. This makes sense in relation to the threats posed by aerial versus terrestrial predators during the repetitive phase of predator encounters. Raptors that are on the ground or in nearby trees visible to colony members, probably have little chance of capturing squirrels since some raptors seem to rely on an undetected approach combined with speed when hunting Columbian ground squirrels (W. King (pers. comm.)). In contrast, terrestrial predators such as coyotes represent a greater danger while they are in the colony even if they have been seen (unpubl. data). Thus, repetitive shrill/harsh chirps probably represent a higher alarm level than repetitive hollow chirps.

My playback experiments revealed no significant differences in alert response to repeated hollow versus shrill/harsh chirps although the same difficulties exist as mentioned earlier in interpreting data from these experiments.

Some species such as S. beecheyi and S. richardsoni appear to specify differential behavior to the initial appearance of aerial versus terrestrial predators through the use of different calls in response to the two types of predators (Owings and Virginia 1978; Davis (in press)). In all likelihood the major information in these calls is still the alarm level (Robinson 1981). The use of predator differentiated calls could reflect a response to different hunting strategies and/or threats by the different predator types (Marler 1977). If true, these predator differences should be consistent in order for the information contained in predator differentiated calls to be reliable.

If aerial predators of Columbian ground squirrels that are visible are less alarming than terrestrial predators, squirrels may be able to return to feeding sooner and move further away from burrows during the repetitive phase of aerial compared to terrestrial predator encounters. However, once the predator has left the area or is no longer visible, the threats posed by

predators should return to pre-attack levels and aerial predators would be at least as alarming as terrestrial predators (Robinson 1981; Turner 1973). Continuing a repetitive call to aerial predators that indicates lower alarm seems like a poor strategy unless aerial predators are less likely to return to the area. Data regarding behavior during the repetitive phase or the likelihood of a predator returning to an area are needed to clarify any selective advantage of giving two types of repetitive calls.

A number of experiments could be used to determine the functional significance of repetitive calling. Vigilance could be measured by comparing head raising, scanning, and alert postures prior to playback with behavior during and after playback. Repetitive calls should be played for at least three minutes and behavior should be monitored for a number of minutes after calling has ended. Lowering of response threshold could be tested by comparing behavior during release of a trained predator with behavior during subsequent releases in order to determine if response time is decreased or whether the predator is spotted sooner.

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Table 1. Summary of available information on repetitive calling in the family Scluridae.

Species	Type of Calls given Repetitively	Remarks	Source
<u>Spermophilus columbianus</u>	hollow, shrill	hollow less alarming than shrill	Betts 76
<u>Spermophilus richardsoni</u>	chirp (unspecified)	given to hawk on ground	Davis (in press)
<u>Spermophilus armatus</u>	chirp (unspecified)	calls continued after hawk left	Balph & Balph 66
<u>Spermophilus beecheyi</u>	chat, chatter	given to hawk on ground or in tree	Owings et al. 78
<u>Spermophilus parryi</u>	whistle	given to hawk on ground	Hannessy et al. 81
<u>Marmota flaviventris</u>	long & short whistle continued after predator left		Malchoir 71
<u>Marmota vancouverensis</u>	whistle, keeaw	whistle to predator, keeaw after predator left	Waring 66 Heard 77
<u>Marmota caligata</u>	call (unspecified)		Noyes & Holmes 79
<u>Cynomys ludovicianus</u>	bark	continued after predator left	Waring 70
<u>C. leucurus</u> , <u>C. gunnisoni</u>			
<u>Tamiasciurus hudsonicus</u>	call (unspecified)	given to perched raptor	Smith 1978
<u>T. douglasii</u>			

Table 2. Frequency, length, and interval between successive calls (mean $\pm$ standard error) for Hollow and Shrill/Harsh repetitive chirps.

	N	Frequency (kHz)	Length (ms)	Interval (s)
Hollow	28	2.5 $\pm$ 0.04	56 $\pm$ 3.30	1.9 $\pm$ 0.17
Shrill/Harsh	14	5.5 $\pm$ 0.06	63 $\pm$ 3.10	2.7 $\pm$ 0.43
Mann-Whitney		p<0.001	p>0.09	p<0.03

Table 3. The number of trials with raptors and dogs in which each of two types of repetitive calls were given.

	Hollow	Shrill/Harsh	Both
Raptor	27	5	2
Dog	0	26	1
Chi Square (2X3) = 41.3 p<0.001			

Table 4. Responses of Columbian ground squirrels to 22 paired playback trials of Hollow and Shrill/Harsh repetitive calls, and responses to unpaired playback of non-repetitive (n=52) and repetitive (n=44) calls. Wilcoxon Signed Rank tests were used for the paired comparison and Mann-Whitney tests for unpaired comparisons. Mean values $\pm$ standard errors are listed. Alert postures were classified on a scale of 0 (no response) to 5 (see text).

	Maximum Alert Posture	Time Spent Alert (s)
Hollow	3.2 $\pm$ 0.17	80.8 $\pm$ 12.3
versus	p>0.1	p>0.1
Shrill/Harsh	3.5 $\pm$ 0.16	64.3 $\pm$ 10.3
Non-repetitive	2.8 $\pm$ 0.11	77.9 $\pm$ 10.5
versus	p<0.05	p>0.1
Repetitive	3.4 $\pm$ 0.12	72.6 $\pm$ 8.1

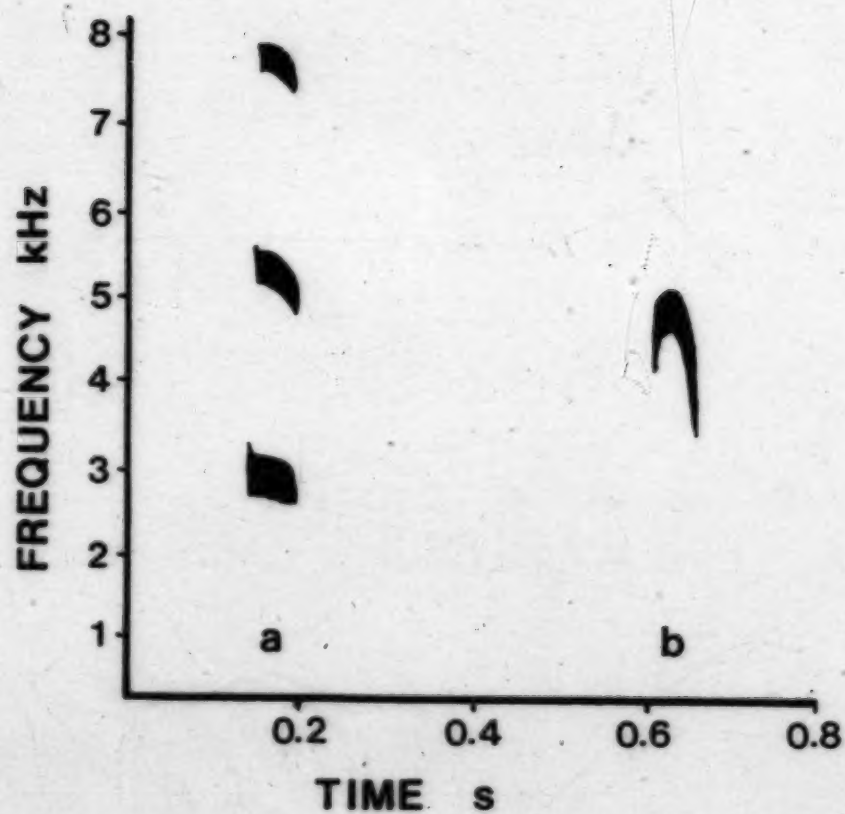


Figure 1. Representative sonograms (wide band) of repetitive calls given by Columbian ground squirrels in response to trained Raptors and Dogs. (a= hollow chirp, b= shrill/harsh chirp).

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III. Paper 3. Responses of Columbian Ground Squirrels (Spermophilus columbianus) to Playback of Predator Elicited Alarm Calls

A. Abstract

Variations in recorded vocalizations given by Columbian ground squirrels (Spermophilus columbianus) in response to the release of trained raptors and dogs were played back to free-ranging squirrels. They responded in a more alert manner to playback of 3 or more calls than to 1 or 2 calls, but did not respond differently to calls with secondary frequencies (harsh) versus a pure note call (shrill). Posture tended to become more erect over time more often to 3 or more versus less than 3 calls and squirrels initially faced at an angle of 80 degrees in relation to the source of the call. Playback results were generally consistent with data collected during predator release experiments.

B. Introduction

Calling in response to predators is a widespread phenomenon among sciurids and these calls have been found to vary in terms of a number of structural parameters. Two general categories of sciurid calling systems can be distinguished.

Some species emit a distinctly different call to aerial versus terrestrial predators (Balph and Balph 1966; Melchior 1971; Owings and Virginia 1978; Davis (in press)), whereas other species do not differentiate according to predator type (Waring 1966, 1970; Schwagmeyer 1980; Lickley 1984a). A third group may be intermediate in that structurally distinct calls are often given to aerial versus terrestrial predators, but the amount of overlap is high (Heard 1977; Robinson 1981).

Playback experiments have been used in some species to determine what information, if any, is transmitted to neighboring conspecifics by these alarm calls (Leger and Owings 1978; Harris et al. 1983). Some squirrel species that give predator differentiated calls respond differently to aerial than to terrestrial predator calls (Leger et al. 1977). In addition, squirrels have been shown to respond in a more alarmed manner to variations in certain call parameters (Leger et al. 1977, 1980; Leger and Owings 1978; Owings and Leger 1980; Schwagmeyer 1981; Harris et al. 1983).

Field experiments involving the release of trained raptors and dogs indicated that Columbian ground squirrels used one basic type of alarm chirp (shrill chirp) in response to the initial appearance and/or attack of these predators. Calls to the two types of predator did not differ significantly (Lickley 1984a). However, these calls varied with respect to the degree of harshness, the number of calls, the length of calls, and the interval between successive calls.

Evidence from these release experiments suggests that these variations were more likely related to the degree of alarm than to the type of predator. In addition, playback experiments by Harris et al. (1983) indicated that Columbian ground squirrels responded in a more alert fashion to playback of a call with unrelated secondary components (harsh shrill chirp) than to a pure note call (shrill chirp).

I conducted a series of playback experiments with Columbian ground squirrels in the summer of 1982 testing the effects of number of calls and harshness in order to determine if these variations were related to the level of alarm response shown by the squirrels.

C. Methods

Alarm calls given by free ranging Columbian ground squirrels in response to controlled releases of a trained red tailed hawk and a black Labrador retriever were recorded during the summer of 1981 at the Ruffatto cattle ranch, 10 km northwest of Stevensville, Montana (46° 35' N, 114° 5' W, elevation 1000m). Recordings were made with a Uher 4000 Report Monitor tape recorder and an AKG 1000 Microphone at a tape speed of 19 cm/s (see Lickley 1984 for details). Calls were chosen for playback based on the quality of recording. They were reproduced in a recording studio to boost and standardize playback levels and to reduce the amount of background noise. Two parameters were selected for paired playbacks.

a) Shrill versus harsh shrill chirps. Shrill chirps (see Harris et al. 1983 for terminology) were single, pure note vocalizations that had no unrelated harmonics (Figure 1a). Harsh shrill chirps had a dominant component similar to shrill chirps plus a number of unrelated harmonics, giving a harsh quality to the sound (Figure 1b). These harmonics varied in their intensity, length, frequency and number. For playback purposes, one harsh shrill chirp with strong unrelated harmonics and a shrill chirp of similar length and frequency were used.

b) Number of calls.

A single shrill chirp (Figure 1a), two shrill chirps given quickly so that they are joined together (double shrill chirp) (Figure 1d) and a series of five shrill chirps given in rapid succession at an average interval of eighty ms between chirps (multiple shrill call) were used during one group of playback experiments. A second group of experiments involved a single harsh shrill chirp (Figure 1b), the same chirp played three times with a 300 ms interval, and a series of six harsh shrill chirps given in rapid succession with an average interval of 50 ms between chirps (multiple harsh call). The multiple shrill call contained chirps from two

squirrels who were calling simultaneously while all other categories were made up of chirps from a single squirrel.

Experimental Procedure.

Playback experiments were conducted at a number of colonies along the Sheep River drainage (50° 38' N, 114° 39' W, elevation 1500m), approximately 30 km west of Turner Valley, Alberta and along the Highwood River drainage (50° 23' N, 114° 39' W, elevation 1500m) 46 km west of Longview, Alberta from 6 May to 21 July, 1982. Playback of single versus multiple harsh chirps were also conducted from 6 to 18 June, 1982 in Montana on the ranch where the predator release experiments took place.

Playback was done from a vehicle parked at the roadside. Squirrels were not marked and age and sex were not known. Trials were conducted on a paired basis (see Table 1 for pairings used) in order to minimize variability in response levels that might be related to changes in environmental conditions or the state of the animal. Calls were played using a Nagra IV tape recorder and a Kudelski Power Amplifier/Loudspeaker (6W class B). The frequency response of this amplifier was flat. Volume of playback pairs was adjusted in each trial according to the distance from the speaker to the squirrel and wind conditions in order that the sound reaching the squirrels would be approximately equal between trials. Responses of one or sometimes two squirrels at a time were noted at each trial. Following playback at one location I moved a minimum of 100 m along the road before commencing the next trial.

I waited until no calling was heard from the area and squirrels were behaving in a non-alert fashion (eg. playing, feeding, grooming) before beginning a trial. Following playback of the first call, the behavior of the squirrel was observed until it resumed a non-alert activity. A minimum of three minutes of silence and non-alert activity was allowed to elapse before playing the second call. The order of calls was alternated so that an equal number of each call was presented first in each playback series.

Responses monitored during a trial included the type of alert postures, the total time spent alert, the direction the squirrel faced relative to the speaker, and whether or not it ran

to or entered a burrow. Alert postures were classed as by Harris et al. (1983) with the exception of category 5 (in burrow, with head and torso out of burrow) (Figure 2). Category 5 was added as the most intense alert posture because I felt that watching from the safety of a burrow reflected a higher alarm level than standing at a burrow's edge in an exposed stretch posture (category 4). Initial posture, maximum alert posture and change in posture were compared. Time alert included the total amount of time spent by a squirrel in all alert postures before resuming a non-alert activity. It was assumed that the higher postures, longer time spent alert, and occurrences of running to or entering a burrow reflected greater levels of alarm (see Harris et al. 1983).

The direction faced by the squirrels after hearing a call was noted and scored as being closest to one of the following; 1 = directly at truck, 2 = a 45 degree angle from truck, 3 = a 90 degree angle, 4 = a 135 degree angle and 5 = directly away from truck (Figure 3). The amount of time spent facing the initial direction prior to changing direction (scanning) was also noted.

Within each playback pair, Wilcoxon signed rank tests were used to compare initial alert posture, maximum alert posture, time spent alert and direction faced by the squirrels. McNemar tests were used to compare running to burrows and change in posture. Where playback trials were combined across the paired design, unpaired comparisons were made between various call categories using Chi Square tests for proportions, Mann-Whitney tests and t-tests for comparisons of means. A probability level of 0.05 or lower was considered significant.

D. Results

Squirrels usually reacted to playback either by assuming an alert posture immediately, or after running to a burrow entrance. Squirrels entered burrows immediately during only 6 of 466 playbacks. Rarely did squirrels call during a trial and never immediately following playback. Occasionally, no visible reaction was noted to one or both of the calls. Since it was impossible to determine whether the lack of reaction was due to having not heard the call,

rather than ignoring it, those trials ($n=7$) were excluded from the analysis.

Alert posture and time alert ($p>0.05$, Mann-Whitney U tests) and number of squirrels running to burrows ($p>0.05$, Fisher Exact tests) were similar for each paired comparison regardless of the order of playback except where noted in Table 1. Since only 6 of 80 playback categories indicated a difference in response with order played, and the direction of differences was not consistent, they could have occurred by chance. Therefore, all calls of a given type were combined for comparisons within paired experiments.

Paired Comparisons

a) **Single harsh shrill versus shrill chirps.** There were no significant differences in any of the parameters measured in response to single harsh shrill versus single shrill chirps (Table 1a).

b) **Number of chirps.** Time spent alert was significantly longer following playback of multiple harsh and multiple shrill as compared to single harsh or shrill chirps (Table 1b, 1c, 1d). In addition, squirrels responded with a significantly higher maximum alert posture, were more likely to increase the alertness of their posture after the initial alert posture, and ran more often in response to the multiple harsh versus single harsh calls during the Alberta experiments (Table 1c). However, these differences were not evident for the multiple versus single harsh calls played in Montana (Table 1b).

The double shrill call received a shorter time spent alert than did the multiple shrill call but no other comparisons of these calls were significant (Table 1e). There were no significant differences in the responses of squirrels to single versus double shrill chirps, or to three versus multiple harsh calls (Table 1f, 1g).

Unpaired Comparisons

The data from the paired experiments were combined and re-analysed on an unpaired basis in order to increase sample sizes and examine the data in ways not included in the paired design. However, one must be more cautious in interpreting these unpaired comparisons. All overall comparisons indicated that alert posture, time alert, running, and increasing posture

with time, were significantly different depending on the number of calls played (Figure 4). A comparison of means between single, double, three chirps and more than three chirp playback experiments revealed significant differences in maximum alert posture and time alert between 1 and more than 3 chirps, but not in any other comparison. (Figure 4a,b). A significantly larger proportion of squirrels ran upon hearing three chirps or more as compared to single or double chirps, but there were no significant differences between single versus double chirps, or three versus more than three chirps (Figure 4c).

Change in alert posture over time was also greater for increasing numbers of calls. A larger proportion of squirrels had an initial alert posture that was lower than the maximum posture in response to trials with more than three chirps versus single chirps (Figure 4d). Double and three chirp trials had an intermediate proportion of squirrels increase posture (Figure 4d).

There were no differences between call types in the direction that squirrels faced after hearing a call, or in the amount of time prior to changing direction (Kruskal Wallis tests, $p > 0.05$). The mean direction faced by squirrels was 2.8 (approximately at an 80° angle in relation to the speaker (Figure 3)).

E. Discussion

In this study, I found no differential alert response to shrill versus harsh shrill chirps. By contrast, Harris et al. (1983) found that Columbian ground squirrels responded with both a higher maximum alert posture and a longer time spent alert to harsh shrill than shrill chirps. Differences in the type of calls used could partially explain the conflicting results obtained in the two experiments. The shrill chirps were similar in all major parameters, but the harsh shrill chirp used by Harris et al. (1983) differed in the interval between, position, and relative intensity of secondary components as compared to the chirp used in this study (Figure 1b, 1c). The harsh shrill chirp of Harris et al. (1983) was recorded from a trapped squirrel at close range and the call was likely in response to the approach of the investigator (M.A. Harris, pers.

comm.). The chirp used in this study was recorded during a Hawk release trial and was representative of the harsh shrill chirps recorded during my predator release experiments in basic structure. Of the over 300 harsh shrill chirps recorded during 80 predator release trials, none resembled the chirp used by Harris et al. (1983). Therefore, perhaps the two harsh shrill chirps are used in different contexts. The chirp of Harris et al. (1983) may be a call given by squirrels in immediate danger of being caught, whereas the chirp used in this study may be more typical of the anti-predator alarm call given by squirrels after initially spotting a predator and when not in immediate danger of capture.

It is also possible that the recordings used by Harris et al. were of a higher quality (ie. less background noise) because they were recorded at close range from captive squirrels. Beechey ground squirrels more often failed to respond to calls recorded in the field than to recordings from captive squirrels (D.H. Owings, pers comm). Perhaps, therefore, squirrels were less able to distinguish between shrill and harsh shrill chirps recorded in the field than to those recorded in captivity.

The results of my predator release experiments indicated that although more harsh shrill calls were given during higher alarm situations, the degree of harshness was not related to alarm level. Therefore, harshness is probably not an overly important indicator of alarm level at least when used singly.

The number of calls appears to produce different levels of alarm. Responses to 3 or more chirps were greater than to one or two chirps (double). Double chirps elicited the same response as single chirps, and squirrels appeared not to react differently to them. This is consistent with the results of my predator release experiments. Low alarm trials rarely elicited more than two chirps (mean = 1.9 (range 1-3) chirps per trial) whereas higher alarm trials rarely received fewer than 3 chirps (mean = 8.8 (range 1-25) chirps per trial). During playback experiments there was no greater alert response to 3 versus more than 3 chirps. Possibly a threshold exists of three chirps at which the alert response reaches a maximum level so that subsequent calls in a series elicit no greater response by the squirrels. The number of chirps also

appears to indicate alarm level in S. beecheyi, but the effect was different for aerial versus terrestrial predator calls. Squirrels responded in a more alarmed manner to a fewer number of aerial calls, while they were more alarmed by a higher number of terrestrial calls (Owings and Leger 1980; Leger et al. 1980).

Leger and Owings (1978) found that S. beecheyi exhibited a different sequence of postures to calls that were more associated with aerial versus terrestrial predators. Terrestrial calls resulted in a higher alert posture during the first minute, with a gradual decline in posture over the next two minutes. The posture in response to aerial calls, in contrast, was greatest during the second minute and was lower in the first and third minutes. They interpreted this as a response to the differential threat and method of attack of the two predator types in that it would be advantageous to assume a low initial alert posture and be as inconspicuous as possible in response to aerial predators that might be swooping low over the colony. A high initial alert posture would enable a squirrel to spot and monitor the usually slower approach of terrestrial predators.

A comparison of the initial alert posture and the maximum alert posture during my playback experiments shows an increase in the alert posture over time with the number of chirps played. However, this was not the case during paired playback experiments. In addition, data from release experiments indicate that an increase in alert posture is most likely not a reaction to predator type.

Betts (1976) stated that Columbian ground squirrels face in the general direction of the caller on hearing a call. In response to my playbacks, 75% of the squirrels faced at an angle of 90 degrees or less in relation to the source of the call. The peripheral vision of squirrels is probably sufficient to allow the squirrel to spot the caller at a 90 degree angle. Scanning usually did not begin until 20 seconds or more after the squirrel had responded to the call. Predator release experiments indicated that squirrels usually oriented toward the predator immediately after its' release. If squirrels do not usually call unless they have spotted the source of disturbance (Harris et al. 1983; Lickley (unpubl. data)), squirrels that have not detected the

predator can probably best assess the initial danger by directing their attention towards the source of the call and observing the behavior of squirrels that have spotted the predator. However, it is probably a better strategy to search for the source of alarm rather than the caller in order to accurately assess the behavioral response necessary.

As with many sciurid species, the alarm calls of Columbian ground squirrels vary with respect to a number of parameters, some of which appear to convey information about the alarm situation to conspecifics. Areas for further study include; the effects of interval between successive calls using controlled comparisons (eg. three harsh calls at a 300 ms versus 100ms interval), an additional test of the effects of two chirps versus three chirps using the same chirp and interval for the comparison, and a test of the effect of length of the call on the responsiveness of squirrels. During all future experiments, a more detailed analysis of behavior in response to alarm call playbacks is recommended, possibly through the use of video taping, in order to further understand the subtleties of the Columbian ground squirrel alarm system.

F. Acknowledgements

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Table 1. Playback results of the effects of harshness (harsh vs. shrill) and number of calls (1, 2, 3, and >3 chirps) on alert responses.

Wilcoxon (paired=a-g) and Mann-Whitney tests (unpaired=h) were used to compare initial and maximum alert postures, and time alert. McNemar (paired) and Chi Square (unpaired) tests were used for % squirrels that ran, and increased posture. (*= $p<0.05$, **= $p<0.01$, ***= $p<0.001$) (+=1st call had greater alert response than 2nd, ++=2nd call greater than 1st (Fisher Exact tests, $p<0.05$)).

	N	Initial Posture	Maximum Posture	Time(s) Alert	% Ran	% Increased Posture
a) Harsh	37	2.5	2.8	51.4	+ 46	30
Shrill		2.6	++ 2.9	47.0	60	38
b) Multiple Harsh	20	2.4	3.0	69.4	++65	36
1 Harsh (Montana)		2.3	2.8	39.0	38	41
c) Multiple Harsh	27	2.7	3.3	69.3	79	47
1 Harsh (Alberta)		2.8	3.0	33.8	38	15
d) Multiple Shrill	23	2.0	2.3	+ 105.8	81	50
1 Shrill		2.3	2.5	43.8	46	19
e) Multiple Shrill	28	2.5	3.2	55.7	80	58
2 Shrill		2.4	2.7	41.0	53	30
f) 2 Shrill	17	2.2	3.1	+ 69.6	+ 61	58
1 Shrill		2.2	2.9	30.6	67	50
g) Multiple Harsh	21	2.3	3.2	75.0	76	52
3 Harsh		2.7	3.5	83.0	85	43
h) Multiple Harsh	68	2.5	3.2	75.6	75	46
Multiple Shrill	52	2.3	2.8	77.9	81	54

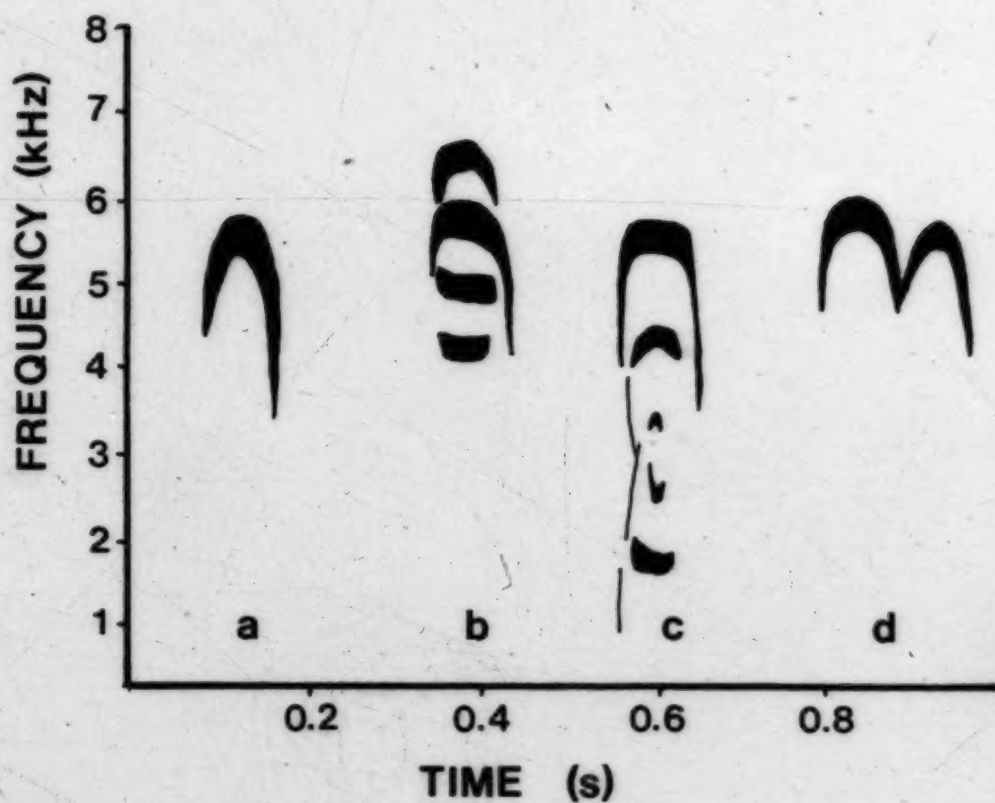


Figure 1. Sonograms (wide band) of calls used during playback experiments. (a= shrill chirp, b= harsh shrill chirp, c= harsh shrill chirp used by Harris et al. 1983, d= double shrill chirp).

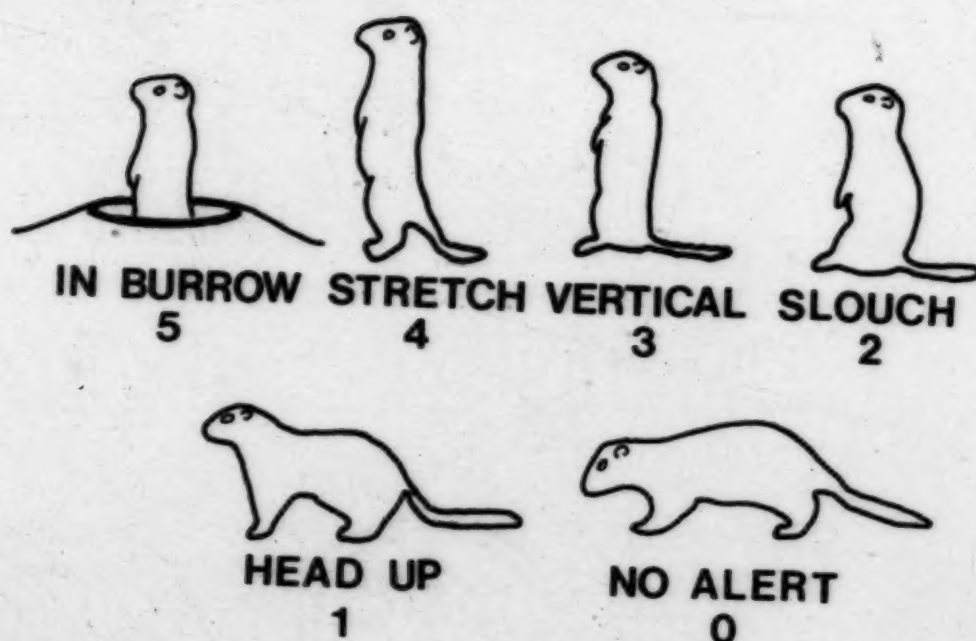


Figure 2. Ranking of alert postures (greater with increasing number) for comparisons of initial alert posture, maximum alert posture, and increase in alert posture during playback experiments. Rankings and postures 0 to 4 are from Harris et al. 1983.

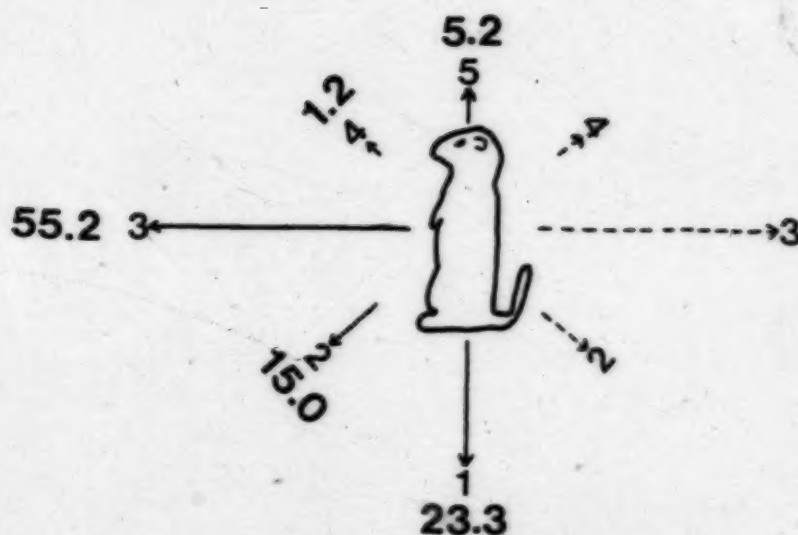


Figure 3. Direction faced by squirrels relative to the source of the call during playback experiments. Direction is ranked from 1 (directly at speaker) to 5 (directly away from speaker). The percentage of squirrels that faced in each direction is given.

a) Maximum
Alert
Posture
 $p < 0.001$

b) Time
Spent
Alert
 $p < 0.001$

c) % That
Ran
 $p < 0.001$

d) % That
Increased
Posture
 $p < 0.01$

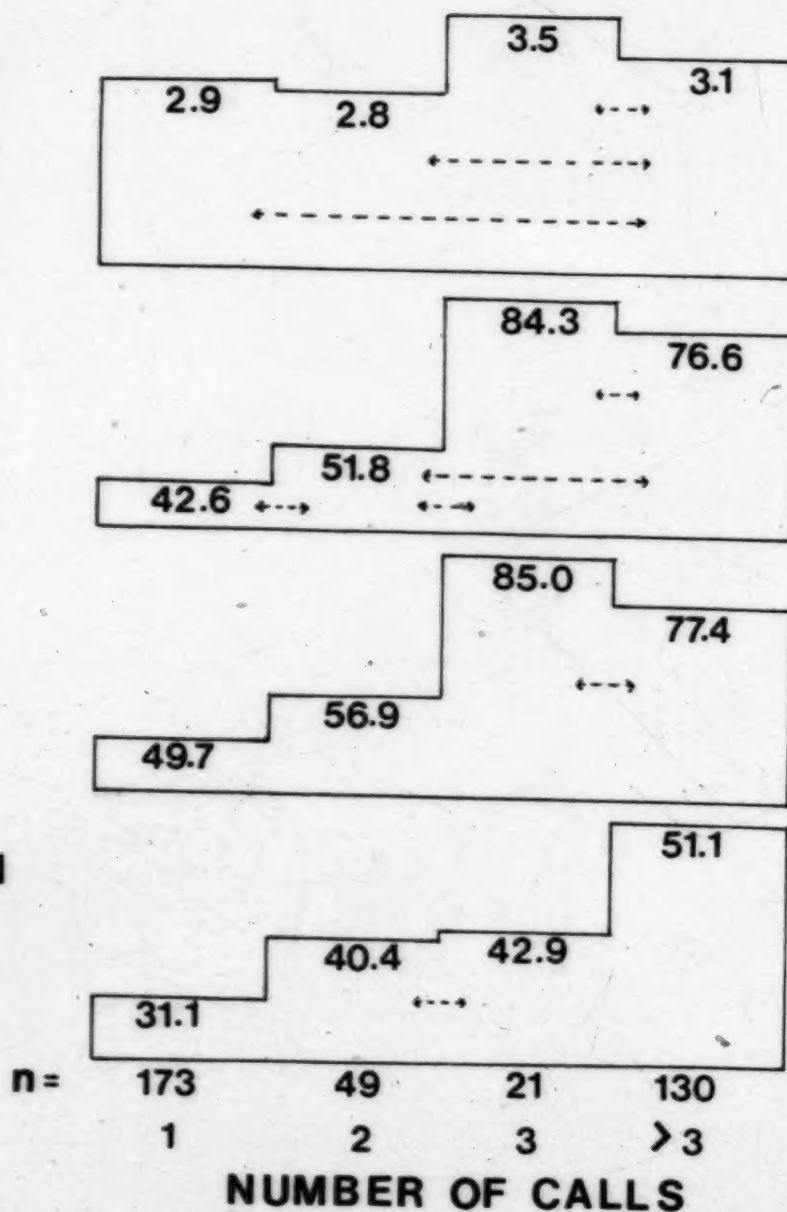


Figure 4. The effects of the number of calls on maximum alert posture, time alert, running, and increase in posture, combining data from all experiments. Kruskal Wallis tests were used for overall comparisons and Newman-Keuls tests for pairwise comparisons of maximum posture and time alert. Chi Square tests were used for running and increase in posture. Non-significant comparisons ($p > 0.05$) are indicated by arrows (--->).

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IV. Concluding Discussion

A number of theories have been advanced about the function of alarm calling in ground dwelling sciurids and about what information is contained in these calls. Generally, it appears that calls warn conspecifics of danger thereby allowing them to avoid capture (Sherman 1977; Owings and Hennessy (in press)). However, the information transmitted by calls may vary with the context. In particular it is important to distinguish between two phases of calling during predator encounters; calls to the initial appearance of the predator, and subsequent repetitive calls both, while the predator is visible and after it has left the area (Owings and Hennessy (in press)).

The information conveyed by calls to the initial appearance of a predator can vary from conveying alarm level only, to more complex information specifying predator type and/or behavioral response (Owings and Virginia 1978; Seyfarth et al. 1980). Ground dwelling sciurids can be loosely separated into two alarm calling groups; those that give different alarm calls to aerial versus terrestrial predators, and those that don't. Columbian ground squirrels belong to both groups. They give different repetitive calls to aerial and terrestrial predators, but they give the same calls to the initial appearance of both predator types.

Calls varied considerably to the initial appearance and some variations appear to be related to the alarm level associated with the predator encounter. Specifically, high alarm releases received more calls, a shorter interval between calls, a shorter length of individual calls, and a higher number of calls containing secondary components (harsh shrill chirps). Playback experiments confirmed that the number of calls affects the alert response. However, a threshold of 3 calls may exist after which no greater alarm response occurs.

The function of calls during the repetitive phase maybe to increase vigilance and monitor predator movements while the predator is visible, and to increase vigilance and lower the threshold of response during subsequent attacks once the predator has left the area (Owings and Hennessy (in press)). However, there is no direct evidence to support these hypotheses.

Columbian ground squirrels are unique among ground dwelling sciurids so far examined in that repetitive calls given to aerial predators (hollow chirps) are different than those given to terrestrial predators (shrill/harsh chirps). Although my playback experiments revealed no differences in alert response to the two types of repetitive calls, other evidence (eg. Betts 1976; Harris et al. 1983) suggests that they may contain information about the alarm level, with hollow chirps indicating a low alarm context and shrill/harsh indicating greater alarm (Betts 1976; Harris et al. 1983).

The reasons for the use of a predator versus non-predator differentiated calling system have not been discussed in other studies. Since Columbian ground squirrels use both systems, they may provide some insight into the question.

It seems probable that alarm calls would differ on the basis of predator type when a different behavioral response is generally used for aerial versus terrestrial predators, or when the alarm level associated with the two predator types is predictably different (Marler 1977)(eg. Beechey ground squirrels (Owings and Virginia 1978); Vervet monkeys (Seyfarth and Cheney 1980)). Thus in order to truly assess the information contained in calls and determine their function, knowledge of predator behavior is essential (Seyfarth et al. 1980).

In Columbian ground squirrels, urgency appears to take precedence over specifying a specific behavior during the initial appearance of a predator, and it is likely that aerial and terrestrial predators generally either present a similar threat, or the danger level is not predictable on the basis of predator type. In contrast, Richardson's ground squirrels give different calls to aerial versus terrestrial predators. The major difference in their reaction to these two predators appears to be that they run first to aerial predators prior to assuming an alert posture, whereas they assume an alert posture first to terrestrial predators and then run if it seems appropriate (Davis (in press)). This probably reflects the urgency of escape during attacks by aerial predators and a consequent consistently higher alarm level. (Columbian ground squirrels also ran immediately more often to aerial releases and this was probably because aerial trials were generally more alarming than terrestrial trials. However, the

difference in running to the two predator types was less consistent than in Richardson's ground squirrels).

The reasons for the difference in calling systems between Richardson's and Columbian ground squirrels may be a function of predator hunting behavior and habitat. Richardson's ground squirrels generally occupy open habitat without surrounding cover and predators are usually visible to the squirrels when hunting. Aerial predators use hovering and soaring, relying on speed to catch squirrels away from burrows. Terrestrial predators such as coyotes probably wander through colony areas, hoping to catch squirrels that stray too far from burrows. Aerial predators, once they begin an attack, probably represent a consistently higher immediate threat to squirrels than terrestrial predators.

In contrast, the habitat of Columbian ground squirrels is generally hilly or mountainous and consists of meadows surrounded by forests. Aerial and terrestrial predators take advantage of this cover to approach colonies undetected and catch squirrels by surprise (W. King (pers. comm.); J. Murie (pers. comm.)). Thus, the threat to the squirrels posed by both predator types may frequently be similar until the predator is spotted. During the repetitive phase the situation is quite different. Raptors that have been seen and are either on the ground or in trees likely represent a consistently lower danger than coyotes that are wandering through colony areas. Hence, the repetitive calls given by Columbian ground squirrels are different to aerial versus terrestrial predators in this context.

The major difficulty with this interpretation is that repetitive calls continue after the predators have left the area. It seems probable that the danger would once again be similar for both predator types, but again data are lacking.

The calling system used by a particular species is presumably a result of selection and would depend on the range of predators the squirrels are exposed to, their hunting techniques (and consistency of them), and the extent to which squirrels enhance their escape by particular behaviors. (This, of course, is based on the assumption that the information conveyed by calls is truthful and aimed at conspecifics (Sherman 1977; Cherry 1979). It is conceivable that

factors affecting selection may differ between species and this must be considered in any comparisons of alarm call systems.

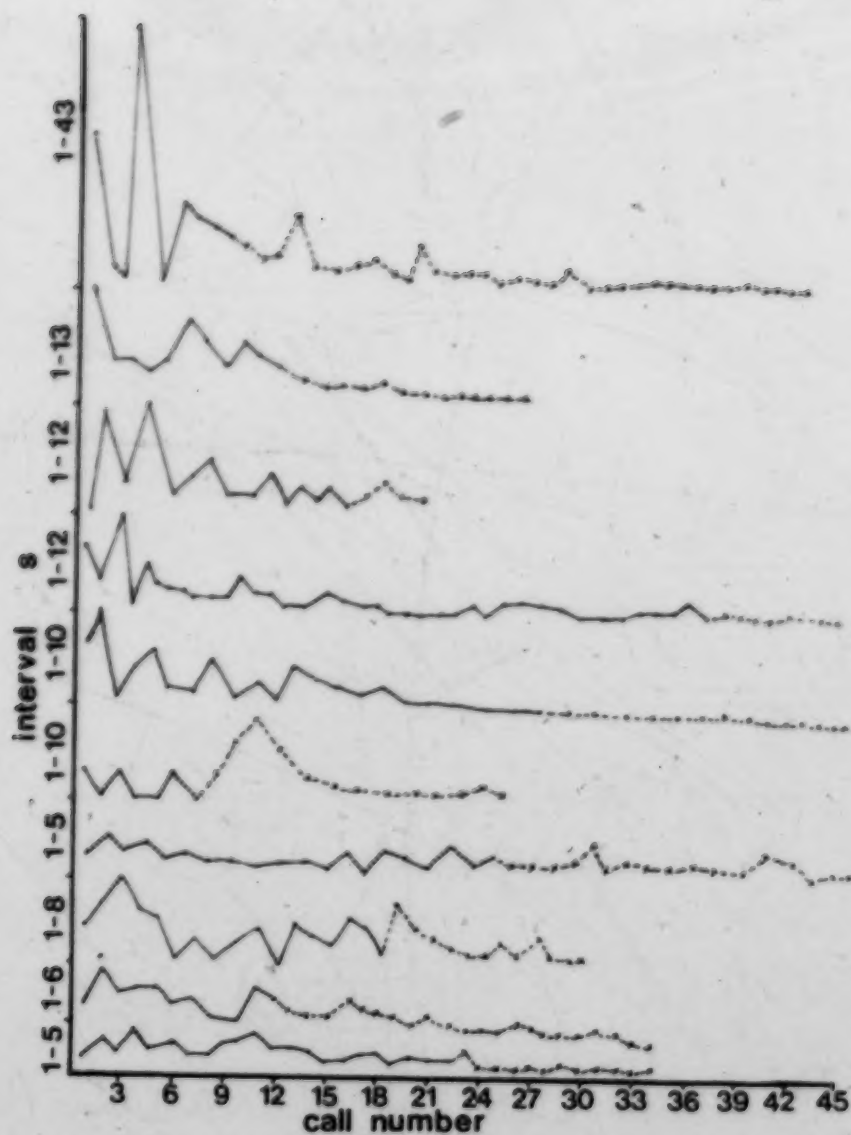
The least known element is predator behavior, especially as naturally occurring predator attacks are infrequently seen during field studies. Predator release experiments, while useful in studying calls and behavioral responses to predator types, yield little information on hunting techniques of predators. The information obtained from experimental releases of predators and playback of calls can provide some information about alarm call systems, but they may not be representative of alarm levels associated with wild predator attacks. Detailed studies of predator-prey interactions are necessary in order to validate interpretations of these results.

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V. Appendix 1. Mann-Whitney comparisons of distance from release site to the colony and time since last trial on the same colony, and Chi Square tests of pre-release alertness and direction faced by squirrels, during Raptor and Fast Dog releases. The relationship between pre-release alertness and running immediately after release (Chi Square) is also given.

	Raptor (n=38)		Fast Dog (n=29)		p
	Mean	± S.E.	Mean	± S.E.	
Distance from Colony (m)	61.7	3.9	51.8	4.0	>0.05
Time Since Last Trial On Colony (days)	1.4	0.3	0.9	0.2	>0.2
% Alert Pre-release	31.8		43.6		>0.1
% Facing Release Site Pre-release	36.1		17.1		>0.05
	Alert		Not Alert		p
% Squirrels that Ran (n=154)	29.8		54.6		<0.01



VI. Appendix 2. Interval between successive repetitive calls given by 10 Columbian ground squirrels during Slow Dog releases while the dog was visible to the squirrels and moving (—), and after it was no longer visible (---). The range of interval for each squirrel is given.